INVESTIGATION OF CORDAITEAN PHYLOGENESIS WITH CORDAITEAN SEEDS

A Senior Scholars Thesis

by

JULIAN EDUARDO CORREA

Submitted to Honors of Undergraduate Research
Texas A&M University
in partial fulfillment of the requirements for the designation as

UNDERGRADUATE RESEARCH SCHOLAR

May 2012

Major: Geology

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Approved by:

Research Advisor: Anne Raymond
Associate Director, Honors and Undergraduate Research: Duncan MacKenzie

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ABSTRACT

Investigation of Cordaitean Phylogenesis with Cordaitean Seeds. (May 2012)

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Cordaiteans are a group of plants present during the Carboniferous and Permian; the group is held together largely by the characteristic leaves. Cordaiteans are gymnosperms (seed-bearing plants). The group includes many genera that are known only from seeds. This creates an inherent problem with describing phylogenetic associations/evolutionary relationships among the different species, since many traits (e.g. traits of the stem, leaves, and cones) are missing. In order to try and make a phylogenetic tree linking all cordaiteans, including those known only from seeds, we developed a traits matrix using only seed and pollen traits. The starting taxa selected for the study come primarily from Hilton *et al*. (2003, Bot. J. Lin. Soc 141: 151-175) "Reinvestigation of *Cardiocarpus minor* (Wang) Li *nomen nudum* from the Lower Permian of China and its implications for seed plant taxonomy, systematics and phylogeny." Taxa known only from immature ovules (e.g. ovules known only from fertile cones) are dropped from the study. Various ways of coding traits were investigated to see the effect of trait coding on phylogenetic trees. Cladistic analysis reveals a strong relationship among the mitrospermeans, while

cardiocarpaleans were less strongly associated. Results suggest that developing a consensus on how to code seed traits would improve phylogenetic trees of ancient land plants.

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I would like to acknowledge Suzanne Constanza for her suggestions and discussion over the course of this study and her translations of the French scientific literature on cordaitean seeds. I would also like to acknowledge Mr. Jian Gong for suggestions and discussion over the course of this study and his assistance in running PAUP.

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CHAPTER I

INTRODUCTION

Cordaiteans represent a key stage in the evolutionary development of gymnosperms (seed-bearing plants). Cordaitean seeds have an integumentary system similar to modern gymnosperms, sealing the ovule at the nucellar beak and at the micropyle after fertilization (Serbet & Rothwell, 1995). Though similar seed integuments have been observed as early as the Upper Devonian, these exhibit hydrasperman reproduction, in which the central columnella seals the ovule after fertilization (Rothwell, 1986). Cordaitean seeds have been found in permineralized peat and ash beds from the Late Carboniferous and Early Permian. Cordaitean seeds are characterized by 180° rotational symmetry; other seed characteristics, such as vascularization, additional symmetries, pollination structures, and integument morphology are also used to distinguish genera and species of cordaitean seeds (Taylor, Taylor and Krings 2009). The pattern of vascularization within the integument determines the generic assignment of cordaitean seeds. Note that these characters (three integumentary layers, post-pollination sealing of the ovule at the micropyle and nucellar beak, 180^0 rotational symmetry) are found in some seeds not previously considered as cordaitean (for example, *Callospermarion* (callistophytalean) and *Plectospermum*).

This thesis follows the style of *Botanical Journal of the Linnean Society*.

The primary challenge in phylogenetic analysis of Paleozoic plants concerns how to deal with plant organs that become disassociated from the parent plant prior to fossilization; paleontologists have few whole plant reconstructions. Other challenges include taphonomic modifications to the fossil, misinterpretations of morphology and characteristics due to studies based on fossils of mutant or diseased organisms and variations in traits due to environmental adaptations, or ontogeny (change in morphology during development).

The basic morphology of cordaitean seeds includes the integument, composed of a parenchymatous endotesta (the inner 'soft' lining of the seed chamber), the sclerotesta (the hard wall of the seed chamber, analogous to the 'shell' of nuts) and a parenchymatous sarcotesta (the soft outer layer of the seed: Fig. 1). This integument has a micropyle, which is an opening at the top of the seed for pollen to gain access to the megaspore, and surrounds the nucellus, a parenchymatous organ, which is the homologue of the megasporangium. The nucellus encloses the megaspore, in which the embryo develops, and a pollen chamber, which is near the micropyle. Once in the micropyle, pollen enters the pollen chamber and sperm from the pollen fertilizes the embryo. Cordaiteans have a double vascular pattern ('veins'). A single vein enters the base of the seed and forms a nucellar plate at the base of the nucellus, which brings water and nutrients to the nucellus and megaspore. The two integumentary veins branch from the vein that enters the base of the seed and bring nutrients and water to the integument (Figure 1). Hilton *et al.* (2003) sought to circumvent this problem by using

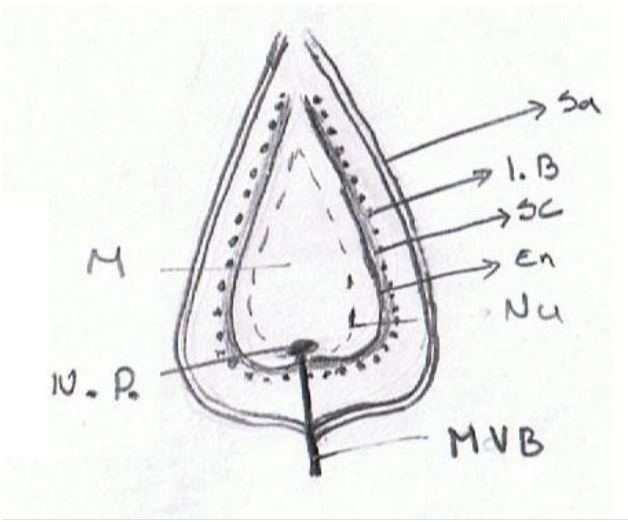

Figure 1. General morphology of cordaitean seeds. M: Megaspore, Nu: Nucellar Sheath, En: Endotesta, Sc: Sclerotesta, Sa: Sarcotesta, MVB: main Vascular Bundle, I.B: Integumentary Bundle, N.P.: Nucellar Plate

permineralized seeds to investigate the phylogeny of cordaitean gymnosperms. This is an innovative approach – modern plant phylogenies are based on reproductive traits. Seeds are complex reproductive propagules and seed coats are often well preserved. Despite the promise of this approach, the results of the Hilton *et al.* (2003) paper were ambiguous. Outgroup callistophytalean seed fern ovules formed a clade with North American *Mitrospermum* species. Furthermore, the addition of *Cardiocarpus angarensis* by Johnson *et al*. (2007) produced a large number of parsimonious trees with low retention and consistency indices. In addition, the bootstrap analysis run for the experiment yielded a giant polytomy between all the taxa.

The inclusion of incompletely preserved specimens and immature specimens may have contributed to the ambiguity of the Hilton *et al.* (2003) result. For example, the

sarcotesta of *Cardiocarpus sclerotesta* is not preserved (Brongniart, 1874), with the result that all sarcotesta traits for this taxon must be coded as missing. Similarly, *Emporia lockardii* seeds are known only from cones and these immature seeds lack a fully developed sclerotesta with the result that many sclerotesta traits for this taxon are missing.

The phylogenetic analysis of cordaitean seeds presented here omits immature and poorly preserved taxa. In addition, Brotzman (1974) and cordaitean seeds from the Thompson-Darrah collection of the Harvard Botanical Museum were used to reevaluate the character states of North American cordaitean seeds. Bertrand (1907 a-d and 1908 a-c) were used to reevaluate the character states of French cordaitean seeds. The goal of this study is to examine several aspects of cordaitean classification using phylogenetic techniques:

1. Should all the seeds with 180° symmetry be placed in the Cordaitales?
2. Do cordaitean seeds from France having the *'Mitrospermum'* vascular pattern form a clade with North American *Mitrospermum* species?
3. Do European, North American and Chinese species of *Cardiocarpus* form a clade?
4. Is the division of *Cardiocarpus* and *Mitrospermum* justifiable?

Phylogenetic tree analysis can be done with any number of programs that run an algorithm routine that creates "parsimonious" (tight attribute) trees. The parsimonious trees link different groups of species into clades. To find the most favorable tree, scientists can either use biological and geological criteria, or 'fuse' the trees using the

common denominators: strict consensus, semi-strict consensus, and majority rule. Each method uses different criteria to determine the best denominators and form consensus trees. Bootstrap or Bremer structure analysis is used to indicate how well the data support the consensus trees.

CHAPTER II

METHODS

The cladistic analysis uses 25 cordaitean ovules (Table 1-pg. 15) recovered from permineralized material from various global locations. The specimens chosen correspond with most of those of Hilton *et al.* (2003) in order to compare how different trait descriptions and trait selection affects phylogenetic trees. The ovules are studied under the microscope after they are processed using acetate peeling technique (Joy *et al.*, 1956). The specimens peeled by the analysis team mostly include North American species such as *Cardiocarpus spinatus, C. magnicellularis Nucellangium glabrum, Mitrospermum florini* and *M. leeanum.* The other taxa are scored based on papers published by scientists responsible for the description and or the discovery of the specimens. The 50 traits (Appendix 1) reflect the anatomy of the vascular system, integument, and reproductive system. The scores are independent of species genealogy and are assessed purely on morphology and anatomy. All the traits are unpolarized or unweighted.

The program used to perform the cladistics analysis is "PAUP: Phyogenetic Analaysis Using Parsimony" a program that runs maximum likelihood and distance methods to grade the scores each species gets with each trait. The analysis runs 1000 to produce a strict consensus and a 50% majority consensus tree; the strict consensus tree is the only tree to be analyzed and accepted for discussion and results: the 50% majority tree was produced for the sole purpose of looking at the effect of traits and trait characterization.

The Bootstrap analysis was run 1000 times and had a 50% minimum acceptance to maintain any of the clades.

Taxa and traits

Three taxa are excluded from the analyses presented here because the sclerotesta or integument is not fully developed in the described specimens (*Mitrospermum bulbosum*, *Emporia lockardii* and *Sergeia neubergii).* In *M. bulbosum* the layers of the integument, the endotesta, sclerotesta and sarcotesta, are undifferentiated, possibly because the specimen is an immature seed, or because this early seed had an undifferentiated integument. When included in the analysis, *M. bulbosum* forms an outgroup with respect to other cordaitean seeds. In the case of *E. lockardii* and *S. neubergii*, incomplete development of the sclerotesta could be a generic trait, however it is far more likely due to seed immaturity. As previously discussed, these seeds known only from ovulate cones, not as dispersed seeds (Mapes & Rothwell, 1991; Rothwell *et al.*, 1996).

Cardiocarpus sclerotesta was excluded because complete specimens, including sarcotesta, have not been found and all the sarcotesta traits must be coded as missing.

The results presented here differ from those of Hilton *et al.* (2003) in part due to new information concerning the anatomy and morphology of seeds included in the Hilton *et al.* analysis. The French cordaitean seeds were scored using Bertrand (1907 a-d and 1908 a-c) translated by S.H. Costanza (Costanza, pers. comm. 2011). With the exception of *Cardiocarpus tritilopus* and *Mitrospermum vinculum*, North American cordaitean

seeds were scored using Brotzman's (1974) Ph. D. thesis and observations of specimens in the Thompson-Darrah Coal Ball Collection of the Harvard Botanical Museum.

A number of traits were reinterpreted from Hilton *et al.* (2003) in an attempt to better reflect the range of character states present in cordaitean seeds. Appendix 1 contains descriptions of each trait and values of the character states. Changes in the coding of traits that had a large effect on the phylogenetic tree are discussed below.

Traits 9 and 10 in Hilton *et al.* (2003) refer to the origin and position of the integumentary vascular bundles with respect to the sclerotesta. These two traits were merged into a single trait with three character states (Trait 9 in Appendix 1), and an additional trait was added (Trait 10 in Appendix 1). New Trait 10 has two character states: integumentary bundles are found entirely in the sarcotesta (0); integumentary bundles found in the sclerotesta and sarcotesta (1).

Hilton *et al.* (2003) interpreted the outer layer of large barrel-shaped secretory cells in the sarcotesta of *Cardiocarpus magnicellularis* as a columnar epidermis (Trait 13). However, in *C. magnicellularis* from the Williamson No. 3 Mine in Iowa, the cells in this layer do not have a uniform size and shape, and the layer itself may be more than one cell thick. Accordingly, we scored *C. magnicellularis* as lacking a columnar palisade (character state 0) for Trait 13.

Scoring Trait 31 of Hilton *et al.* (2003) depends on having a good basal cross-section, or sections in the major and minor plane through the middle of the seed. Because these are not available for all taxa, this trait was omitted from the analysis.

Trait 31 of Hilton *et al*. (2003) was replaced by a new trait, parenchymatous chambers in the sclerotesta, with two character states: absent (0), present (1). This trait occurs in some of the French cordaitean seeds with a '*Mitrospermum*' integumentary vascular pattern' and in North American *Mitrospermum* species.

Hilton *et al*. (2003) included seven traits (Traits 35 through 41) associated with post-pollination sealing of the ovule (e.g. hydraspermum versus cordaitean post-pollination sealing). These post-pollination sealing traits included much missing data. In the present analysis, these seven traits were simplified into two traits: Trait 47, post-pollination sealing mechanism with two character states, hydraspermum (0), cordaitean (1); and Trait 48, pollen type with three character states, trilete (0); Florinites (1); Vessicaspora (2). Because the pollen type of many French cordaiteans remains unknown, Trait 48 had a number of missing values.

CHAPTER III

RESULTS AND DISCUSSION

The preliminary results reveal a different phylogenetic tree from that produced by Hilton *et al.* (2003). This difference is due to changes in the taxa used and differences in the trait scores as discussed above.

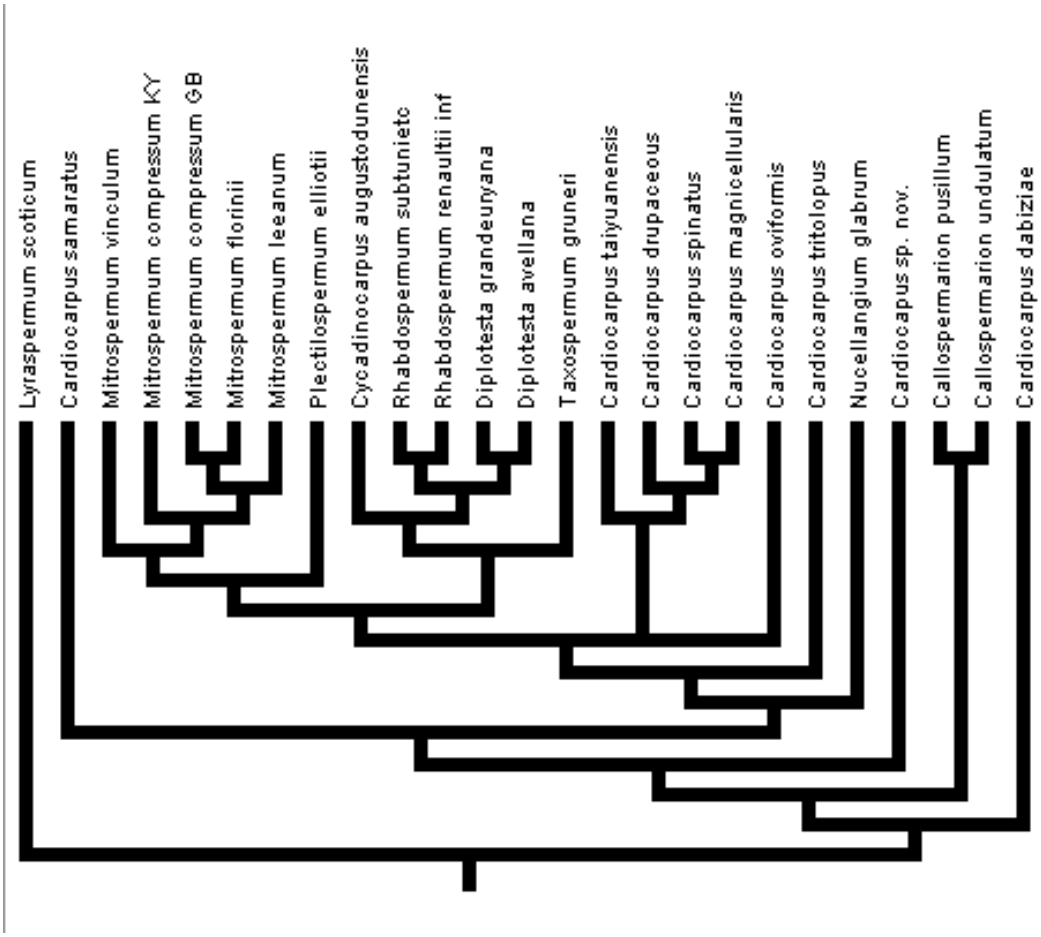

Figure 2. Strict consensus tree. The arrangement above represents the primary arrangement of the taxa after the experimental runs. It came from 6 parsimonious trees.

The resulting analysis yielded 6 parsimonious trees; all trees consistently returned 3-4 clades (Figure 2): 1) a *Callospermarion* clade, which formed an outgroup with respect to all cordaitean seeds except *Cardiocarpus dabiziae*; 2) a *Mitrospermum* clade consisting of French seeds with a '*Mitrospermum*' vascular pattern, North American species of *Mitrospermum* and *Plectilospermum*. Within this clade are two smaller clades consisting of French seeds with a '*Mitrospermum*' vascular pattern and North American *Mitrospermum* plus *Plectilospermum*; 3) a small Cardiocarpus clade including two North American seeds, *C. magnicellularis* and C. spinatus, as well as C. drupaceous (from France) and *C. taiyuanensis* (from China); 4) occasionally, additional species of *Cardiocarpus* formed a fourth clade.

Lyrasperma scotia acts as the out-group for the phylogenetic tree. This seed shares bilateral symmetry with cordaitean seeds, but has a hydraspermum post-pollination sealing mechanism. In analyses including *Mitrospermum bulbosum*, this seed also formed an outgroup with respect to all other seeds in the analysis except *Lyrasperma scotica*.

In the Hilton *et al.* (2003) results *Callospermarion* seeds formed a clade with North American *Mitrospermum* species. With a few exceptions, the French seeds with a 'Mitrospermum' vascular pattern formed a clade. Within this clade, both species of Diplotesta formed a clade. However, this clade also included two North American seeds with a cardiocarpalean vascular pattern, C. magnicellularis and Nucellangium glabrum.

The Bootstrap results yeilded a giant polytomy (Figure 3). Four smaller clades are embedded in this polytomy: 1) the two Callospermarion species; 2) the French seeds with 'Mitrospermum' vascular patterns; 3) North American Mitrospermum species; and 4) Two North American Cardiocapus species, C. magnicellularis and C. spinatus. Hilton *et al*. (2003) did not publish a bootstrap analysis. However Johnson *et al*. (2007)

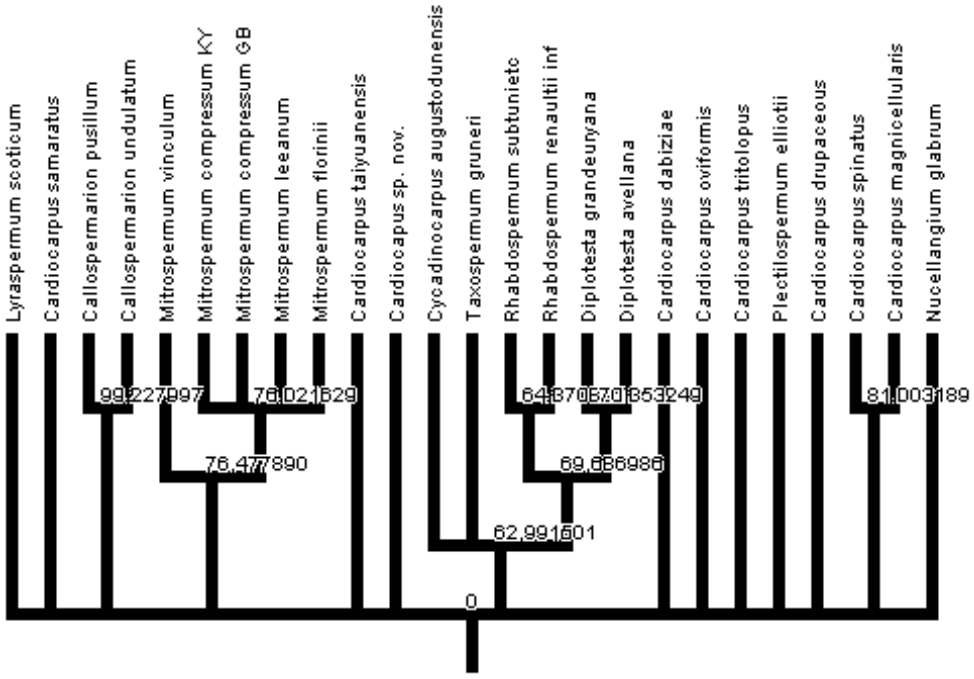

Figure 3. Bootstrap analysis. The Bootstrap displays a giant politomy with a few clades forming. It only retained clades with 50% majority.

published a bootstrap analysis of the Hilton *et al*. (2003) data set plus one new species, Cardiocarpus angarensis. This bootstrap analysis yielded a giant polytomy with two embedded clades, the two Callospermarion species and the two Diplotesta species.

CHAPTER IV

SUMMARY AND CONCLUSIONS

The results of the strict consensus tree confirm most of the hypotheses listed in the Introduction. Based on this result, seeds with 180° symmetry and cordaitean post-pollination sealing mechanism belong to the Callistophytaleans (Callospermarion) or the Cordaitales. However, early conifer seeds included in the Hilton *et al*. (2003) analysis (Emporia lockardii and Sergeia neubergii) were eliminated from this analysis because they were not fully mature when fossilized. It seems likely that some early conifer seeds also had 180^0 rotational symmetry and a cordaitean post-pollination sealing mechanism. The results presented here suggest that the '*Mitrospermum*' vascular pattern unites French and North American cordaitean seeds as well as *Plectilospermum* from Antarctica. The parent plant of *Plectilospermum* is not known; however a cordaitean affinity for this seed should be considered.

As both Hilton *et al*. (2003) and Johnson *et al*. (2007) discussed, the trait that characterizes the genus *Cardiocarpus*, its integumetary vascular pattern, is primitive. Not surprisingly, *Cardiocarpus* species from China, France and North America did not form a clade. Two North American species, *C. spinatus* and *C. magnicellularis* form a consistent clade in our strict concensus and our bootstrap tree; observer their similarities in Table 1. Brotzman (1974) hypothesized that these taxa were sister species. However, few characters appear to be unique to either North American or to the Chinese species of *Cardiocarpus*.

The fact that seeds with the ‘Mitrospermum’ vascular pattern form a consistent clade in this analysis suggests that the separation of Mitrospermum and Cardiocarpus is justified. However, genera in addition to *Mitrospermum* are included in the ‘*Mitrospermum*’ clade and the phylogenetic position of *Cardiocarpus* species remains unresolved.

One thing notable about the results of this study is the bootstrap analysis. Bootstrap analysis yielded a polytomy preventing further conclusions since a polytomy of this level is inconclusive. While researching possible interpretations of such a bootstrap result, I discovered that bootstrap analysis is the preferred method for the study of modern organisms. Modern phylogenetic analyses have access to hundreds of thousands of traits due to genetic data, and the bootstrap method was developed to help interpret that level of data. Paleontological phylogenetic analyses only have between 40-80 traits since the characters come from observations of the anatomy of the taxa. With so few traits, the results of most bootstrap analyses are difficult to interpret. I also discovered a secondary analysis termed Bremer analysis. This analysis works by deconstructing a clade and giving it a value based on how many steps it took to deconstruct. Bremer analysis could shed more light on these results and it is the next step in this research.

Table 1: Character Matrix

	L. scoticum	*C. samaratus*	*C. pusillum*	*C. undulatum*	*M. vinculum*	*M. compressum. UK*	*M. compressum.* KY	*M. leeanum*	*M. floriniii*	*C.taiyuanensis*	*C.* sp. nov.	*C. augustodunensis*	*C. dabiziae*	*C. oviformis*	*C. tritoloputus*	*P. elliotii*	*C. drupaceous*	*C. spinatus*	*C. magnicellularis*	*T. grunerii*	*N. glabrum*	R. renaultii	R. subtunicatus	*D. grandeuryana*	*D. avellana*	–	
1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
2	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	3
3	1	1	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	1	0	1	1	1	1	3	4
4	0	0	0	0	0	0	0	0	0	0	2	2	2	0	0	0	0	0	0	0	0	0	0	1	1	4	5
5	0	4	4	4	2	1	2	1	1	3	?	3	3	3	4	2	3	3	3	4	4	4	4	3	3	5	6
6	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	6	7
7	0	0	1	1	1	1	1	1	1	0	0	1	0	1	1	1	1	1	1	0	1	1	1	1	1	7	8
8	0	1	0	0	0	1	1	1	1	2	1	2	0	1	0	0	0	1	1	1	1	1	1	1	1	8	9
9	0	0	1	1	2	2	2	1	2	0	0	1	0	0	0	2	0	0	0	2	0	2	2	2	2	9	10
10n	0	0	1	1	1	1	1	1	1	0	0	1	0	0	0	1	0	0	0	1	0	1	1	1	1	10n	11
11	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	11	12
12	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	2	2	2	2	12	13
13	0	0	0	0	0	0	0	0	?	0	0	2	0	0	0	0	0	0	0	0	1	1	1	1	1	13	14
14	2	0	3	3	2	2	2	2	2	0	0	1	0	0	2	0	1	1	1	0	0	0	0	0	0	14	15
16	0	0	1	1	0	0	0	0	0	0	1	?	1	0	0	0	0	0	0	0	0	0	0	0	0	16	16
17	0	1	0	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	17	17

Table 1 Continued

18	0	0	0	0	0	0	0	0	0	0	1	1	2	0	0	1	0	0	0	1	0	1	1	1	1	18	17
19	0	1	1	1	1	1	1	1	1	1	1	2	0	1	1	1	1	1	1	2	1	1	1	2	2	19	18
20	0	1	0	1	2	1	1	2	1	1	0	0	0	2	1	1	1	2	2	0	1	1	1	1	1	20	19
21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	21	20
22	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	22	21
23	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	23	22
24	0	0	0	0	1	1	1	1	1	0	0	1	0	1	1	1	1	1	1	1	?	1	1	1	1	24	23
25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	25	24
26	0	0	0	0	0	0	1	1	?	1	0	0	0	0	0	0	1	1	1	0	1	0	0	0	0	26	25
27	1	0	0	1	0	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	27	26
28	0	1	0	0	1	0	0	0	0	1	1	0	0	0	0	0	?	0	1	1	0	1	1	0	0	28	27
29	0	1	1	1	1	1	1	1	1	0	0	0	0	1	0	1	1	1	2	1	0	1	0	1	1	29	28
30	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	30	29
31	0	0	0	0	2	1	1	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	31	30
31 A	0	0	0	0	0	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	1	31 A	31
32	?	1	0	0	0	0	0	0	0	0	0	?	0	0	1	0	1	1	0	0	1	1	1	1	1	32	32
33	0	1	1	1	?	?	?	2	2	1	1	?	1	2	?	?	?	2	2	?	2	2	2	2	2	33	33
34	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	34	34
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38	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1	1	1	1	1	1	1	1	1	38	38
40	0	1	1	1	1	?	?	1	1	1	?	?	1	1	?	?	?	1	?	?	?	?	?	?	?	40	39

Table 1 Continued

41	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	41	40
42	2	2	3	3	2	2	2	2	2	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	42	41
43	1	1	1	1	1	1	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	43	42
44	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	44	43
45	0	?	0	0	?	4	4	4	4	1	0	3	0	1	1	?	4	2	2	3	3	3	3	3	3	45	44
46	0	1	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	46	45
47	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	47	46
48	0	?	1	1	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	48	47
49	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	49	48
50	0	4	4	4	1	1	1	1	1	3	4	1	3	1	?	?	1	1	1	4	3	4	4	3	3	50	49
51	0	?	2	2	1	1	1	1	1	1	1	?	?	1	1	?	?	1	1	?	1	?	?	?	?	51	50

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APPENDIX 1

		Traits Worksheet										
			Character state									
col in matrix	trait number	Trait	0	1	2	3	4	Notes		0	1	2
1	1	symmetry	one mirror plane - bilateral	two mirror planes , 180-rotational symmetry								
1	2	integumentary micropyle	absent	present								
3	3	cordate base	a>b	a=b, a<b	we tended to take authors word for this			why is cordate base scored as 0? - this is what Hilton et al. did. we tended to take authors word for this				
4	4	in cross-section, a central concavity in the minor plane	none	some, Diplotesta, Cycadinocarpus	Hilton coded C. tuberculatus, C. dabiziae, and Cyacinas 2							
5	5	commissure	absent	apical slit	present throughout most of the length			defined as apical slit. We have redefined this character as a slit or zone of weakness in the sclerotesta to accommodate germination, but can't code for most seeds	5 alt	seed not closed - slecrotesta does not encase seed cavity - Lyrasperma	commissure involving integumentary vascular trace	commissure is zone of weaknes s in cell
6	6	nucellus fused to integuement	distal from chalaza	at chalaza only				distal is>15% of nucellar length (see text) Is fusion above the chalaza a derived condition? Lyginopterids fused, cordaites, medulloans are not.				
7	7	nucellar tracheal disk	absent	present				vascular pad is 1.5X wider than incoming vascular strand, consider coding if author describes feature as a nucellar tracheal disk.				

			Character state									
matrix	number	Trait	0	1	2	3	4	Notes		0	1	2
8	8	vascularized nucellar sheath	absent	present near chalazal	present distally							
9	9	integumentary bundle departs	from nucellar bundle, before passing through the sclerotesta	from nucellar bundle, within the sclerotesta	after passing through the sclerotesta, from sides or bottom of nucellar pad, or nucellar bundle			see traits sheet sketches				
10	10 new	integumentary bundles	remain in sarcotesta	pass from sclerotesta to sarcotesta				we could treat this as a redefinition of trait 10				
	10	integumentary bundles pass sclerotesta	once	twice				many ovules whose integumentary bundles never pass the sclerotesta coded as 0. EXCLUDED TRAIT				
11	11	integumentary bundles recurved - i.e. depart tracheal disk or nucellar bundle at angle between 0 & 70, and then turn toward micropyle	no	yes				Cordaiteans with condition 9-1 and 9-2 have both straight (11-0) and recurved (11-2) integumentary traces				
12	12	Integumentary bundle shape in cross-section	round	radially elongate: plate, ellipsoid, or multiple strands	tangentially elongate			consider adding condition 2				
13	13	columnar epidermis	no	yes				Hilton et al considered that the secretory cells of C. magnicellularis were a collumnar epidermis. We do not. **Get picture for the paper.**				

			Character state									
matrix	number	Trait	0	1	2	3	4	Notes		0	1	2
14	14	integumentary wing -rib combo trait	no wing	little ridge	wing throughout length	wing apex only		Use 14, 42 or 43. These three are variants on this trait. Could score of Nucellangium=1 based on Brotzman's comment that vascular bundle? or something causes Nuc to have a ridge marking the commisure. I have seen this ridge				
	15	not used										
15	16	sarcotesta has irregular outline	no	yes				Hilton coded this as 1 for C. spin, Cycadino, C. dab. and one Callospermar.		not entirely sure how differs from 23		
16	17	layers in sarcotesta	no	yes								
17	18	Thick walled cells in sarcotesta	none	pitted or sculpted cells	thick walled non-mucellaginous			trait has been redefined from Hilton et al.; it seems we have coded this differently than Hilton et al.		H.et al. 0=present, 1=absent		
18	19	orientation of sarcotesta cells	radially oriented	all isodia or axially elongate	tangentially elongate			Lyrasperma, Plectilo and C. dab have radially elongate cells in sarcotesta; tangentially elongate cells is a French mitro trait - try without special code for radial				
19	20	Sarcotesta with secretory or mucilage-filled cells	absent	present								
20	21	Secretory cells of two types	no	yes				we tried this trait to replace best to say Hilton et al. trait 21. It did not work. Currently known only from Nuc. Glabrum. Look for this in other N.Am cardiocarpids				
21	22	secretory glands	absent	yes				Hilton coded as 0=none, 1=present inner surface (Callospermarion), 2=present outer surface (dabiziae, Cycadin). SHC suggests Cycadin glands are in sclero. Try coding Dabiz and callo differently				

			Character state									
col in matrix	trait number	Trait	0	1	2	3	4	Notes		0	1	2
22	23	small protruberances on outer surface of sarcoteata	absent	yes				Callospermarion trait				
23	24	layered sclerotesta	absent	present				Hilton coded 0=no, 1=indistinct, 2=distinct, but did not score any taxon as 2				
24	25	spinose sclerotesta	no	yes				Hilton coded oviformis as spiny - we did not.				
25	26	sclero with pitted, sculpted cells	absent	present				look at our codes, there is a thin line between this trait and pitted sarcotesta cells				
26	27	sclero with axially elongate cells redefine as: sclero with axially elongate inner layer of cells?	absent	present				our coding of this trait is the same as Hilton - who said 0 absent, 1 present		ck this may be 1's all the way down in our data matrix		
27	28	sclerotesta thickens distally	absent	present								
28	29	Sclero rib in major plane	absent	rb	wing			Hilton did not code wing of C. tritilopus				
29	30	sclero rib in minor plane	absent	present								
30	31	chalazal sclero collar	absent	ridge	collar			trait omiited, requires x-section at base of seed, or exact major, minor plane sections				
31	31a	parenchya chambers in sclerotesta	absent	present								
32	32	endotesta	uniseriate	biseriate				trait omitted -likely developmental				
33	33	distally elongated endotesta cells at micropyle	absent	present								
34	34	nucellus wall	thick	thin				ck if omitted - likely developmental				

			Character state									
matrix	number	Trait	0	1	2	3	4	Notes		0	1	2
35	35	apex of meagspore membrane	round	w/ tent pole				replaced with trait 47				
36	36	Pollen chamber	large	small				replaced with trait 47				
37	37	Membranous pollen chamber floor	present	absent				replaced with trait 47				
38	38	central columnella	present	absent				replaced with trait 47				
	39	central columnella sealing	present	absent				replaced with trait 47				
39	40	post pollination sealing nucellar apex	absent	present				replaced with trait 47				
40	41	post pollination sealingintegument	absent	present				replaced with trait 47				
41	42	trait 14 integumentary wing without character state 1	absent or small ridge	wing throughout length	wing apex only			Use 14, 42 or 43. These are 3 ways to code one trait.				
42	43	trait 14 with only two states	absent	wing or 1/2 wing				Use 14, 42 or 43. These are 3 ways to code one trait.				
43	44	sclerotesta lignification	throughout	sclero flexible or has layers without lignin				possible Nucellangium - C. tritilopus trait - but does not help analysis at this point				
44	45	new 27 wall type	single layer axially elongate	double layer axially elongate	inner isodia, outer axially elongate	inner axially elongate, outer thick, isodia	Mitrospermum	New Trait - Orientation of cells in layers of sclerotesta. Do not use with 27				

			Character state									
matrix	number	Trait	0	1	2	3	4	Notes		0	1	2
45	46	fertilization syndrome including pollen	hydrasperm um	cordaitean with no pollen tubes	cordaitean with pollen tubes - Callosperm arion			New Combo Fertilization Trait - To code this trait, we would have to assume that no cordaitean had pollen tubes. Replaced by 47ck# and 50 ck# NOT USED		1 for Nucellangium, Plectilospermum, tritilopus, taiyuanenesis, **add drupaceous?**		
46	47	post pollination sealing	hydrasperm um	cordaitean				This trait replaces Hilton et al. 2003 traits 35-41				
47	48	pollen tube	no tube	tube				New Trait - To code this trait, we would have to assume that no cordaitean had pollen tubes. NOT USED				
48	49	ovule has closed sclerotesta encasing seed chamber	absent	present				new trait				
49	50	alternate coding of trait 5	valves of sclerotesta not joined	sclerotesta split by vascular bundle mid seed	sclerotesta split by vascular bundle at apex	specialized zone of dehiscence	none	New trait - alternate coding of trait 5. NOT USED				
50	51	pollen, prepollen morphology	small, trilete	monosaccate - Florinites and related genera	bisaccate - Vesicaspora			This trait has a lot of missing data but helps to separate Callospermarion from Cordaitean seeds				

Appendix Notes:

Key to color codes

same as Hilton et al.

omitted trait

try this

reinterpreted w/respect to Hilton etal

replaced by one reroductive trait

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